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LONG-CONTINUED DETERMINATIVE ORTHOGENETIC SERIES.*

STUDIES IN DETERMINATE EVOLUTION, IV.

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There are many evolutionary movements which continue consistently and progressively from the very beginning to the highest possible level, right through a series of the fundamental subkingdoms and often in a number of distinct lines. These determinative movements show that the evolution is not primarily dependent on any special kind of environment nor on any peculiar type of organization. All special teleological notions are immediately dissipated when one once clearly grasps the real import of such consistent progressions.

1. EVOLUTION OF THE PARASITIC INTER-RELATION OF THE TWO GENERATIONS IN THE ALTERNATION OF GENERATIONS CYCLE.

In the lowest plants with an alternation of haploid and diploid generations, all individuals carry on an independent existence. There is no parasitic inter-relation of one generation on another. Such a condition is present in the brown alga, Dictyota. But certain red algæ show the first stage of a parasitic sporophyte in that the fertilized egg or zygote is not discharged or separated from the parent plant but germinates by budding and produces a number of diploid carpospores. This developing zygote of numerous diploid cells represents the first step in a parasitic relation which becomes very prominent in the higher plants. The carpospores are discharged and each one develops an independent sporophyte. Such a condition is represented by the well-known Polysiphonia. In Batrachospermum the zygote develops into a vegetative,

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branching sporocarp of considerable size, the carpospores being developed at the ends of the branches.

The complete parasitism of the sporophyte is attained in the living bryophytes. The lowest stage is represented by Riccia where, after a parasitic vegetative development, the entire sporophyte except the epidermal layer is transformed by reduction divisions into spores. As one passes through the bryophytes one meets successively higher types of sporophytes, each stage representing a progression toward partial independence of the sporophyte which, however, never loses its parasitism in any phase of its life.

The decided advance is attained on the level of the lowest living pteridophytes where the parasitism of the sporophyte is restricted to the juvenile phase, the individual gradually growing into an independent individual. All of the pteridophytes, both homosporous and heterosporous have the two-phased condition of the sporophyte. Step by step the importance of the independent phase is advanced until in the heterosporous pteridophytes, the independent mature sporophyte not only nourishes itself but provides a complete supply of food in the spore both for the gametophyte and for the juvenile life of the following sporophyte which is thus nourished through the mother gametophyte on food provided by the sporophyte grandparent.

In the next stage of advancement the gametophyte becomes completely parasitic on the sporophyte, and while the following sporophyte is passing through its parasitic phase it is nourished by its mother gametophyte with food furnished directly by the grandparent sporophyte. This is a decidedly progressive improvement over the previous method of furnishing a supply of nourishment to the dependent gametophyte and its offspring.

In this state the parasitic relation between the two generations has reached its determinate limit. In the angiosperms a further complication is added in a new evolutionary movement which supplies a xeniophyte, which from one point of view is simply a further elaboration of the parasitic inter-relations of the generations. The gametophyte is enormously reduced and the embryo is surrounded by the xeniophyte which functions as nurse to the sporophyte especially during the sprouting period. This development is, however, not because of any compelling necessity, since very many angiosperms have very little endosperm and the food is stored directly in the embryonic sporophyte.

Now this whole movement constitutes a most remarkable progression which keeps a straight course through all the numerous advancing lines of higher plants, through all the diversity of environments. It continues in a progressive march until the goal is reach. If we wish to see an altruistic ending, it is plainly on the surface because this progressive movement has not only taken care of the reduced and helpless gametophyte but it has also taken the embryo sporophyte and continued it in the most advantageous condition in relation to the struggle with the environment. In these respects the highest plants have evolved in the same way as the highest animals, including mammals and birds, and some reptiles, insects, spiders, and fishes in which the most remarkable evolution in the care for the young has taken place, which care is entirely absent in the lower animals as it is in the lower plants. This long-continued evolutionary movement in the dependent relationships between the two generations is, therefore, remarkably consistently progressive, orthogenetic, perfective, and determinative. It has been carried to the limit.

A consideration of the preceding series will show how untenable are the claims that parasitism or dependence leads to degeneration or reduction. Just the opposite came about. The independent generation passed through a reduction series and at last became parasitic only after the reduction had reached an extreme degree of minuteness. The completely parasitic generation, altho it never lost its juvenile parasitism, evolved step by step attaining independence in the mature condition until we have a giant Sequoia 30 ft. in diameter, 300 ft. in height, and 3000 years of age.

2. The Shifting of the Reproductive Process From the Center of the Stem or Bud to the Outside.

The Meta-thallophyta present a very interesting orthogenetic evolutionary series in respect to the shifting of the reproductive activity of the sporophyte. In Riccia and Ricciocarpus, the lowest forms, the entire center of the stem or body is involved in the production of spores. In the higher liverworts, not only is the lower part of the sporophyte sterilized but the first indication of a movement of the reproductive tissues toward the outside is in evidence by the development of sterile cells or elaters in the interior of the sporangium among

the sporogenous cells. In the true mosses and horned liverworts a completely vegetative columella is differentiated, the sporogenous tissue forming a cylinder within the cortical layer. Now in the evolution from a bryophyte condition to the condition of the living vascular plants, before lateral leaf appendages appeared, the sporogenous tissue must have been developed in the outer parts of the stem just below the epidermis, and even after leaf appendages were present sporangia might still be produced from the external stem tissues or at least in the leaf axils, as in some lycopods. Apparently in such primitive vascular plants like the fossil Psilophyton the sporangia were still developed at the tips of stems as in the higher living bryophytes. But in the lines which are represented by living pteridophytes, the reproductive center was shifted entirely to the lateral appendages and sporangia are borne on the leaves from the ferns on up. The shifting of the sporogenous center from the stem axis or terminal bud to a lateral appendage was one of the main factors in the evolution of indeterminate sporophytes, although with the introduction of a branching system, either dichotomous or monopodial, indeterminateness could be attained for the sporophyte as a whole even though some buds still were destroyed through the development of terminal cauline sporangia as in Psilophyton.

The movement of the reproductive process toward the periphery of the plant does not involve the epidermal layers in most of the higher evolutionary lines. In one series, however, the leptosporangiate ferns, the movement attained the extreme limit in that the sporangia are not only produced on the stem appendages or leaves but from the very epidermal layer of cells itself. Thus the orthogenetic movement has reached the determinate limit in these plants. In the lowest forms, like Riccia, the entire system except the epidermis is involved in spore reproduction, while in the leptosporangiate ferns the epidermis alone is involved in the reproductive process all the remaining tissue systems continuing permanently in the vegetative state. The movement has progressed from one extreme to the other.

In all other higher plants, however, the eusporangiate condition is normally maintained and the epidermis does not take part in spore production. The sporogenous cell is normally a sub-epidermal cell of the first layer from which the sporocytes finally develop. The reproductive process, however, continues

in its centrifugal movement with the evolution of a monopodial branching system and determinate floral axes. The first flowers of the living seed plants are terminal on the main axis, as in Cycas, Dioon, etc. The continuation of vegetative growth is then from an axillary bud beside the cone. But in plants like Macrozamia and its relatives sporophylls appear only on secondary axes, both carpellate and staminate cones being developed in the axils of foliage leaves. With a further evolution of the branching system the reproductive process is shifted out still farther so that the sporophylls appear only on tertiary, quaternary or still more extreme axes, as in Araucaria, various palms, yuccas, etc. With the introduction of vegetative and short-life evolutionary processes in the higher plants, the reproductive process may undergo a recession and may finally appear again on appendages of the primary axis. But this is a new evolutionary movement changing the former gradients and may in itself show an orthogenetic progression.

3. Progressive Recession in the Development of the Archegonium.

In the liverworts and mosses the entire archegonium is differentiated from a papillar outgrowth extending above the general surface of the plant. From this position there is a consistent retrogression as one goes upwards through the higher plants until the entire structure is developed internally. This movement goes parallel with the progressive reduction of the gametophyte but is not necessarily dependent on the movement. In the Anthocerotæ, which have well-developed gametophytes, the differentiation of the entire venter with the egg and ventral canal cell takes place in the internal tissues below the general level of the surface and only the neck is differentiated from the papillar outgrowth. Here then, as in so many evolutionary movements, the process of differentiation gains on the ontogenetic development and thus the initiation of the given differentiation process takes place in successively earlier and earlier stages of the ontogeny. In this case the movement is also in agreement with the evolutionary reduction of the gametophyte but is not to be interpreted as being primarily due to this cause, since exactly similar movements take place in other morphological systems where no reduction of the individual is in evidence.

In the homosporous pteridophytes, the venter always has an internal development and the neck of the archegonium is in general much shorter than in the bryophytes. In the heterosporous pteridophytes the neck consists of but a few cells extending beyond the general surface, while in the gymnosperms there is practically no papillar outgrowth whatever, the few remaining neck cells being on a level with the general surface of the body or nearly so and range from eight down to two, except in the Gneteæ. In this highest class of gymnosperms there may be three or more tiers of cells but they do not project above the surface and are not really a true neck but a new structure, something like a tapetal layer. In the angiosperms also the archegonium or egg apparatus is reduced to the extreme limit. Either there is nothing left of the ovary except the egg and ventral canal cell (polar nucleus) or the two synergids represent the last vestige of a neck. In the lower forms there is a long row of neck canal cells and these are gradually reduced to zero, there being but one in the heterosporous ferns and none in the gymnosperms. The evolution of the archegonium thus again shows a consistent orthogenetic, progressive movement through the last five subkingdoms of plants. The general movement has not been disturbed by any of the great segregative movements, resulting in phyla and classes, which have taken place in the evolution of the Meta-thallophyta.

4. The Five-fold Parallelism of the Orthogenetic Progression in the Time of Sex Determination.

In the lower multicellular algæ the sexual states are developed only in the very last cells of the ontogeny, the male and female gametes often being sister cells. From this condition, as one ascends the evolutionary ladder of the sexual plants, the time of sex determination with a dimorphism of sexual states and structures is projected backwards step by step in the ontogeny until the extreme is reached and the sex is determined in the egg, the entire individual being then, of course, normally in a single sexual state. This orthogenetic progression is in evidence both in various series of haploid green algæ and in diploid brown algæ.

In the Meta-thallophyta a similar movement takes place in the evolution of the gametophytes of both the bryophytes and homosporous pteridophytes. The lowest stage present is the

synoicous hermaphroditic condition where sex is determined in the incipient gametangia. From this condition the progression leads through to the paroicous and various degrees of the autoicous condition until in the highest forms unisexuality is attained in numerous lines. The higher plants have all attained the extreme limit, namely all the heterosporous pteridophytes, gymnosperms, and angiosperms. The movement to unsexuality has a definite limit in the spore from which the gametophyte comes. But a new evolutionary series is still possible in the shifting of the time of sex determination backward into the sporophyte itself. This condition initiates a new orthogenetic movement which travels through the ontogeny backwards until the zygote is reached completing the fourth parallel evolutionary movement in respect to time of sex determination.

In the lowest type of heterosporous sporophytes the sexual state is determined in the incipient sporangia and from this condition the time of determination progresses backward through forms with monosporangiate sori, monosporangiate sporophylls with one or the other sexual state determined in the incept of the organ, through the normal bisporangiate flower with maleness determined in the flower bud first and then femaleness, through a series of more and more extreme monecious types, until the determinate limit is reached in the normal diecious condition. The progressive series from bisporangiate flowers to dieciousness is repeated many times in the seed plants including both gymnosperms and angiosperms.

In the higher fungi a truly remarkable sexual condition is established in the evolution of an incomplete primary sexual state. In some of the highest Phycomycetæ as well as in a few of the lowest Ascomycetæ the male and female nuclei, after copulation of the cells, do not immediately fuse but sometimes there is a long delay in this process. This delay is to be attributed to an incomplete primary sexualization for the time being of the nuclei involved. In some of the lower Ascomycetæ vegetative divisions take place before the nuclei finally pass to the complete primary sexual states. These cell divisions are conjugate divisions which occur in such a way that each daughter cell normally receives a pair of the conjugate nuclei. The time of incomplete primary sex determination soon begins an evolutionary retrogression through the ontogeny of the fungus in the same general manner as has been described above for the time of secondary sexual state determ-

inations in the gametophyte and sporophyte series. At the extreme evolutionary limit, as in some smuts and in some of the Gasteromycetæ, the determination is shifted back to the basidiospores themselves which thus copulate and the binucleate or conjugate phase is established in the mycelium at the very beginning of its development. In the extreme homothallic species the first two sister nuclei which arise from the basidiospore nucleus become sexualized with the incomplete primary sexual states and act as a pair of conjugate nuclei. Thus not only is the entire mycelium normally made up of binucleate cells but the process of external copulation at the initial point is entirely eliminated. Nothing like an external conjugation remains in the system outside of the process which takes place in the formation of clamp connections.

In respect to the time of sex determination, there are thus five distinct orthogenetic evolutions or progressions which have evolved independently in five fundamentally different plant constitutions.

1. The movement in the green algae with a simple haploid sexual cycle.
2. The movement in the brown algae with a simple diploid sexual cycle.
3. The movement in the higher fungi in the time of determination of incomplete primary sexual states.
4. The movement in the haploid gametophyte of homosporous plants with typical antithetic alternation of generations.
5. The movement in the diploid sporophyte of heterosporous plants with typical antithetic alternation of generations.

One cannot help but be impressed with this remarkable five-fold parallelism. It is a truly marvelous condition and shows conclusively that fundamental evolutionary movements are not dependent on accidents of morphological differences nor on accidents of physiological and ecological relations. The evolutionary principle lies deep down in the fundamental nature of the living substance itself.

5. Orthogenetic Series Representing Increase of Difference or Divergence of Character Between Sporophyll and Foliage Leaf.

In the specialization of the sporophyll, there is a remarkably uniform progression from the lowest stage where there is no apparent difference until the most extreme divergences are reached at the ends of the various phyla. Among the many series available only a few which can be easily studied will be considered. Many of the lower leptosporangiate ferns, in

which the sporophylls are not on a determinate axis, show no divergence whatever from the foliage leaf while among the higher species a greater and greater degree of difference is developed. In such extreme species as *Onoclea sensibilis* there is a decided dimorphism. The same movement is seen in the carpels of the Cycadales, in passing from the low forms, like *Cycas revoluta* to species of Zamia. In the conifers, the lower groups and species, like Araucaria, have very leaf-like sporophylls while the higher groups and species, like Juniperus, have blue or reddish fleshy cones in which the carpels differ enormously from the foliage leaves. The same serial movement is repeated in the angiosperms. Some Magnolias have rather prominent foliaceous tips. These carpels are probably the most leaf-like of any in the angiosperms. When one proceeds to the highest types there is the merest vestige of a correspondence with the leaf. The divergence is extreme. Thus there is plainly a continuous, progressive movement in the complexity of reactions in the leaf, proceeding from a reaction that shows no difference whatever between sporophyll and foliage leaf except for the presence of sporangia, to the condition in which the differentiation reactions are so extreme that practically all correspondence is obliterated. Again these movements show no relation to peculiarity of morphological or physiological conditions nor to any peculiarity of environment. The movements simply plough their way upward from the bottom to the top.

6. Orthogenetic Evolution of Determinateness in the Floral Axis.

The lowest living pteridophytes have only indeterminate axes, the bud continuing vegetative growth after the production of sporophylls. Flowers, or determinate reproductive shoots, are evolved at various levels in the several phyla. In the Lepidophyta and Calamophyta, flowers appear in the homosporous level. In the fern series no flowers apparently evolved in either the homosporous or heterosporous levels until the seed condition was established. All the living angiosperms and all the living gymnosperms have flowers except the carpellate plants of Cycas and the single species of Ginkgo, including both staminate and carpellate plants. We see then that the flower evolved independently in several lines and that some

groups attained a high level without acquiring the determinate potentiality. The evolution is dependent neither on a definite stage of advancement nor on any particular morphological or physiological acquirement impelling to its appearance. Nevertheless, in nearly all lines, the flower does appear before the end of the series is reached. The first appearance of the determinate property, on which floral development depends, is marked by a rather imperfect mode of action as well as by decided slowness of action in bringing about the stopping of growth. Thus lower flowers often proliferate, namely, continue to grow later as a vegetative shoot, as can be seen especially in various species of Lycopodium, Equisetum, Araucaria, Larix, and Rosa. Because of extreme fluctuation also of the time of determination the number of sporophylls varies greatly. From this condition the evolution of a greater definiteness and greater promptness of determination soon becomes evident as one ascends the ladder of general advancement. Thus the cones of the lower species of Equisetum fluctuate more widely than the more advanced species. In Selaginella, the lower species, like *S. rupestris* terminate the growth of the floral axis very tardily, the bud continuing to produce sporophylls for a very long period, while species belonging to the higher groups, like *S. kraussiana*, stop growth very promptly. In every flower-producing phylum, the same movement is clearly in evidence. In Cycads the lower species have cones with very large numbers of sporophylls while in the highest the numbers are much smaller. In the Strobilophyta the evolution of the flower passes to a very extreme limit of promptness in cessation of growth. In some araucarians, as in *Araucaria brasiliensis*, the staminate cone has about 1000 stamens. As one passes up the series to the more highly evolved types the number is reduced step by step until the limit is reached. *Araucaria cookii* has about 400 stamens on the cone, *Pinus strobus* about 200, *Podocarpus sp.* about 70, *Taxus canadensis* about 7, *Ephedra trifurca* 5, *Gnetum latifolium* 2, *Gnetum gnemonoides* 1. It is impossible for the determinate movement to proceed farther unless epigyny were introduced and this did not occur in the gymnosperms.

In the angiosperms exactly similar movements occur in various phyletic lines. Some of the lower monocotyls have more than 1500 sporophylls in a single flower and the fluctuation is very great. Among the various lines which attain the limit

with a single stamen or a single unilocular ovulary with 3, 2, or 1 stigmas, either with the hypogynous or epigynous condition, the following are characteristic. In the hypogynous Helobiæ, Naias has one stamen; in the eipgynous series Vallisneria has two, or one divided into two halves; in the Spadicifloræ some species have single stamens; among the grasses, some species of Andropogon have one stamen; in the epigynous Scitaminales Canna and other genera have half a functional stamen left; in all the higher orchids there is a single stamen.

The same conditions evolve many times in the dicotyls, although more commonly the limit is two stamens or rarely two half stamens as in Salvia. The most extreme determinateness appears in the higher types of epigyny, where, although the number of sporophylls may not necessarily be reduced to the extreme limit, the center of the flower bud or flower axis actually stops growing before any floral organs have developed. This is possible because the floral organs are lateral appendages and can be developed from the cortical tissue around the center even though the growth of the center has ceased. Thus the culmination in the main evolutionary movement of the flower has been attained. If the bud stops growing before the floral parts appear the possible limit has certainly been reached. No further evolution in the given direction is possible in passing from complete indeterminateness to the extreme of determinateness. This acquirement, through progressive degrees of greater and greater promptness in the process of determination, of the floral axis brings us face to face with the serious aspects of the fundamental nature of evolution. It brings into clear view the reality of the proposition heretofore made that evolution is perfective and essentially determinative. The entire evolutionary history of the flower in its main characteristics shows a universal, progressive orthogenetic, movement which makes its way through the conditions of environment to the very limit. The limit is essentially the same whether, through other evolutionary movements, the plant has in the meantime progressed under the water, or into the desert. When one studies the taxonomic series, one is profoundly impressed with the orderly forward movements of all fundamental evolutions. The persistent reduction of the floral axis is especially impressive since it can be observed in so many different and independent phyletic lines.

7. Evolution of the Lateral Bud System of Woody Plants.

The sporophytes of the liverworts and mosses have a single terminal growing bud. When this bud is destroyed through sporogenesis, the individual begins to die. In the Pteridophyta two types of branching systems are evolved, the dichotomous or bud-twinning system and the monopodial or lateral-bud system. In the main series, many ferns still have practically nothing except the single growing apex. Among the rhizome ferns, sporadic lateral buds and finally branches are usually produced. Now this origin of lateral axillary buds in the main series of higher plants forms another orthogenetic, accumulative movement which can be traced upwards with a fairly constant progression. Among some of the cycads, only a few sporadic branches are produced while in the more highly evolved stem of Ginkgo, along with the addition of an internodal potentiality, a double system is present. Part of the time the more primitive heredity is in operation in a bud when it develops a dwarf branch on which normally no axillary buds are organized, and part of the time the buds develop with the new internodal potentiality in activity when a functional lateral bud is organized in each leaf axil.

The evolution of lateral buds can be followed to good advantage in the conifers. In Araucaria the leaf axils of the main stem do not develop functional buds except at rhythmical intervals. After a zone of stem is developed without buds, suddenly a ring of functional buds appears which immediately produces a whorl or zone of lateral branches. These branches also show sporadic development of buds in their leaf axils. Thus the main stem develops comparatively few functional axillary buds. Passing upward toward the higher conifers, as in Abies and Picea, the rhythmical development of zones of axillary buds continues; but sporadically many axils develop functional buds and branches between the successive, rhythmically developed bud zones. In the lower pines, the succession of whorls of branches is much the same as in the araucarians, spruces, and firs, but all the leaf axils in between also develop functional buds which give rise to small, determinate dwarf branches. The same development of axillary buds and dwarf branches takes place on all the long branches. Thus in pine every leaf axil on the main shoot and long branches produces

functional buds except the winter bud scales. Presumably the winter or resting bud was evolved before the general bud-development-potentiality was introduced. The dwarf branches also produce no functional buds, thus recapitulating the more primitive condition as in Ginkgo. Now in the higher species of Pinus many of the buds between the successively developed whorls of main branches also grow out into main branches and so these higher types become much less symmetrical in form than the lower types. On the various advancing levels of other series, the movement is also toward the production of more and more functional buds, and commonly more branches, until the limit is reached with a functional bud in each leaf axil. Going up to the typical woody dicotyls, one finds a functional bud normally in every leaf axil produced on the entire tree excepting the axils of the scale leaves of the resting bud. The movement is thus carried out rather consistently and the progression is from sporophytes with a single terminal growing bud to more and more numerous axillary buds until the extreme is reached with every vegetative axil developing a bud. This movement when carried out without the interference of other potentialities which might inhibit the growth of buds into branches results then in the evolution of a more and more complex branching system, from no branches whatever to such species among the conifers as *Juniperus virginiana* and *J. barbadensis*, or among the dicotyls as *Ulmus americana* and *Fagus grandifolia*, where the branch and twig system attains enormous complexity. Of course, evolutionary movements may and do arise in the higher series which run counter to this developmental capacity and thus simplifications may appear in the plant body. These simplifications, however, do not indicate simplification of the fundamental hereditary potentiality of the cell but rather, in practically all cases, the simplification and reduction of structures are brought about by actual advancement in complexity of the hereditary potentiality or reaction system. One such interference is the movement toward shortening of the life of the individual down to an annual. In such cases then an annual individual, on rejuvenation and prolongation of growth activity, may develop a much more complicated branching system than usual.

8. Evolution of the Pollen-tube.

The pollen tube represents a new development brought in with the evolution of the seed habit in the higher plants. The pollen-tube, morphologically, simply represents the bulging out of the top cell of the antheridial wall in preparation for the discharge of the male cells. Since the general trend of the heterosporous pteridophytes is toward the evolution of parasitic gametophytes, it is easy to see how the tip cell of the vestigial antheridium could be involved in the acquisition of a parasitic habit. From fossil evidence it appears that in the first stages of seed evolution, the ovule or megasporangium broke open entirely, while the female gametophyte was growing as a parasite within, in much the same way as in the more primitive condition when the megaspores were discharged. The pollen-grains that happened to lodge in this break would thus come near to or in contact with the surface of the female gametophye and the sperms would be discharged into the open and finally find their way down through the exposed necks of the archegonia. As the parasitic habit was evolving, the pollen-tube partook of the parasitic nature. Now when the ovule progressed in accordance with its own evolutionary trend and the ovule finally failed to develop a complete break in the nucellus, the pollen-tube, through its parasitic property, was able to penetrate the small amount of tissue, being guided, no doubt, by a more or less definite sex-reaction, initiated in the female gametophyte below. Thus on penetrating through the tissue below the pollen chamber, the sperms were discharged into the depression into which the necks of the archegonia opened. This condition is present in our living cycads, as in *Cycas revoluta*. Now an orthogenetic movement is on the way, and as one passes up the various phyletic lines of seed plants, a more and more efficient pollen-tube is encountered until the parasitic growth attained is truly marvelous, both as to extent and rapidity of development. Such a complicated evolution as the origin and development of the pollen-tube, along with all the other remarkable advances in the evolution of the seed habit, is understandable on an orthogenetic progressive principle, while on any teleological basis of utility and advantage to the individual, the whole subject takes on a fantastic aspect.

In the highest species of the living Cycadophyta, *Ginkgo biloba*, the pollen-tube development is of the same general

nature as in the cycads. In all plants above this level, the pollentube always penetrates to some distance into the female gametophyte. In the conifers there is no pollen chamber, the last vestige of a dehiscing megasporangium being obliterated, so the parasitic development of the pollen-tube begins on the surface of the nucellus and grows down until it reaches the venter of the archegonium into which the nonmotile sperms are discharged. The parasitic nature of the pollen-tube has increased very greatly in the Angiosperms so that a very long development precedes the growth through the nucellus. The tube grows through the stigma and style, enters the micropyle, and, after penetrating the female gametophyte, discharges the two sperms. One of the most extreme developments is in Indian Corn, *Zea mays*, where the pollen-tube grows down the very great length of the silk in about 32 hours. The highest expression of the parasitic ability of the pollen-tube is probably met in such plants as various species of the Amentiferæ where the efficiency of the tube is so great that it is able to penetrate directly through the side of the ovule or through the chalazal region, as in Casuarina, Ulmus, etc. In this respect as in many others, the Amentiferæ represent a high stage of evolution and not a primitive condition as is implied in their common placement at the base of the taxonomic dicotyl series. The irrational taxonomy still commonly in vogue is one of the chief hindrances in the understanding of correct evolutionary movements. Some of the older arrangements would require the complete re-creation of the species or group before any evolution could even be postulated aside from the hap-hazard or anarchistic kind, for which witches and fairies alone could be responsible. In the evolution of the pollen-tube we have, therefore, another important, orthogenetic progressive series which keeps a definite forward march along with other progressive movements that have taken place in the seed plants.

9. Orthogenetic Advancement in the General Complexity of the Life of the Sporophyte.

Not only are there definite progressive movements in the various morphological systems of the individual but the life of the individual taken as a whole shows the same characteristic progression. In Riccia, the lowest type of liverworts, the entire life of the sporophyte is spent within the confines of the

archegonium venter. In Marchantia and other liverworts there is at first a period of internal development and then the outer end of the individual breaks through the venter and development continues to maturity with existence in the external world. In the higher mosses there is not only an external existence but a functioning phase of various important physiological processes, like photosynthesis and transpiration. In Anthoceros a long-continued growth activity is added, which is continued even after spore maturity has begun. In the homosporous pteridophytes the important indeterminate phase is added to the complexity of the life history. In the seed plants there is not only a double-phased existence, but a definite resting period with subsequent sprouting or re-awakening is added to the complexity of the life of the sporophyte. Thus it is evident that these general conditions of life also represent progressive accumulations, each potentiality or set of potentialities being added to the system thus far evolved. The evolutionary process is a duplicate in a general way of the ontogenetic process through which the individual is developed, with an important difference, however. For while the ontogeny is a progressive awakening to activity of the potentialities present in the cell, the phylogenetic or evolutionary process consists of the definite addition of new potentialities through which the orthogenetic series is unfolded. The higher sporophytes, therefore, have all of the processes and accidents of life which all the lower and intermediate forms possess collectively, namely, (1) internal development, (2) external development, (3) independent functioning, (4) functioning after reproduction, (5) two-phased life, (6) resting period between phases, and (7) re-awakening after rest, or sprouting.